The spines of Fouquieria *

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The six species now comprised in the genus *Fouquieria* occupy collectively a region extending from the vicinity of the City of Mexico northward into California, Arizona, New Mexico and Texas. Nearly all of the species find their habitat in arid districts, and the localities from which they have been reported may be comprised within the southern extensions of the Chihuahuan and Sonoran deserts. Among other adaptations, the various species exhibit a capacity for casting off the leaves during seasons of drought, more or less irrespective of the time of the year, while some interesting features of the formation and casting away of the bark have been noticed.

All of the species bear strong spines and seem to be included under the single colloquial name "ocotillo" by the Mexicans, who use the living plants for hedges and sometimes erect barriers by thrusting the ends of heavy branches into the ground in rows. Messrs. Coville and MacDougal report having seen shrubs of *Fouquieria splendens* planted within a few inches of young shade trees in the streets of Alamogordo, New Mexico. The spreading spiny branches were held in a cylindrical clump around the trunk of the tree by means of wire and formed a most effective protection against damage by animals.

During the course of some recent work upon this genus, Mr. G. V. Nash called my attention to the unusual manner in which the spines were formed, which he described as "developed within the petioles of the leaves on the new growth, becoming apparent when these fall." † The general anatomical facts presented seemed of sufficient interest to warrant a detailed examination, and the results of my observations upon *Fouquieria splendens* and *F. Macdougalii*, specimens of which are growing in the conservatories of the New York Botanical Garden, are presented below.

* The results described in the following paper were obtained by the aid of a Research Scholarship in the New York Botanical Garden, in 1903.

† Nash, G. V. A revision of the family *Fouquieriaceae*. Bull. Torrey Club, **30** 449. 1903.

On the lower side of the petiole of the primary leaves, a woody thickening is developed (FIGS. 11 and 12, *w*) which increases in firmness as the leaf matures. This arises from the cortex, which even in the bud is proliferated to form a thickened area on the outer side of the base of each leaf (FIG. 1, *c*). As the leaf emerges from the bud a conical portion of the cortex on the lower side of the petiole begins to lose its parenchymatous character. The cells lengthen, their ends become pointed (FIG. 2, *s*) and their walls thicken; these changes are accompanied by a diminution in their lumina (FIG. 3, *s*). With phloroglucin and hydrochloric acid they take the violet color characteristic of sclerenchymatous cells. The conversion of the parenchyma into sclerenchyma is incomplete in *F. splendens*, and a slender cone shaped mass of thin-walled cells extends about two thirds of the distance from the base toward the tip of the newly formed spine. This is illustrated by the diagrams of longitudinal and transverse sections shown in FIGS. 4, 6 and 7, *p*. About the time when the leaf-blade is cast off, the parenchyma-core disintegrates and a hollow spine remains. In *Fouquieria Macdougalii*, on the other hand, almost the entire mass of the cortex on the outer (lower) side of the petiole is transformed into sclerenchyma, making a solid heavy spine (FIGS. 5 and 8, *s*).

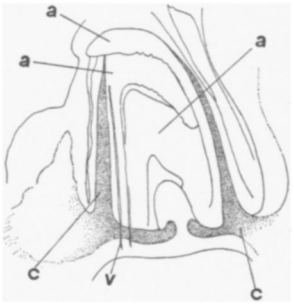

FIG. 1. Section through bud. *a*, young leaf; *c*, cortex, thickened to form spine; *v*, vascular tissue.

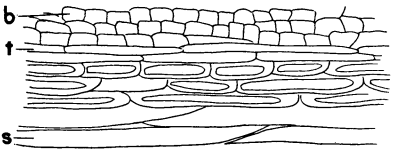

FIG. 2. Portion of longitudinal section through petiole. *b*, cortex; *t*, separating layer; *s*, sclerenchyma.

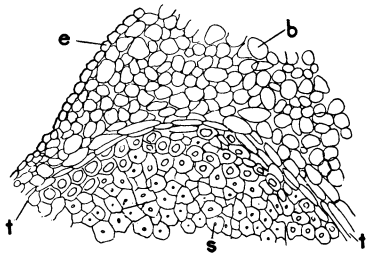

FIG. 3. Portion of transverse section through petiole.

The growth of the leaf and the development of the spine is accompanied by the differentiation of a separatory layer of thin-walled, elongated cells (FIGS. 2 and

3, *t*) in the cortex, between the sclerenchymatous tract and the fibrovascular tissue of the petiole. The sclerenchymatous tissue sustains only mechanical relations to the leaf, and the lamina may be held for extended periods after the completion of the separatory layer. When the vegetative season reaches its end by reason of drought or low temperature, the leaf-blade is cast off; and as its fall occurs simultaneously with its drying out, this desiccation may be taken as the direct cause of the splitting of the separatory layer above mentioned. The separation is identical with that which occurs in the fall of the leaves of many deciduous trees in the autumn in general procedure, but the author is not acquainted with any other instance in which the petiole is cut in a longitudinal plane making necessary a separatory layer two or three centimeters

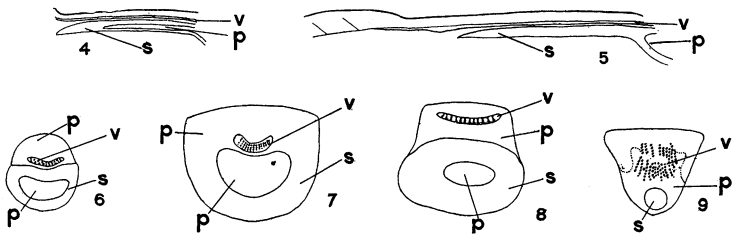

FIG. 4. Diagram of longitudinal section through petiole of *Fouquieria splendens*. *p*, parenchyma; *s*, sclerenchyma; *v*, vascular tissue.

FIG. 5. Diagram of longitudinal section through petiole of *Fouquieria Macdougalii*.

FIG. 6. Diagram of transverse section through petiole of *Fouquieria splendens* near the apex of spine.

FIG. 7. Diagram of transverse section through petiole of *Fouquieria splendens*, near base.

FIG. 8. Diagram of transverse section through petiole of *Fouquieria Macdougalii* near base.

FIG. 9. Diagram of transverse section through petiole of *Fouquieria Macdougalii* near the apex of spine.

in extent (FIG. 13, *d*). Again, this unique method of excision results in leaving an elongated pointed portion of the petiole 3 or 4 cm. in length attached to a mass of thickened epidermis and cork on the stem where it is retained rigidly for an indefinite period. The spine and the contiguous portion of the outer tissues of the stem may easily be pulled from the underlying tissues in *Fouquieria Macdougalii* (FIG. 10, *k*) when they are young, but in *F. splendens* they are less yielding.

In *Idria*, another genus of the same family, a similar spine, originating in the petiole of the leaf, has been described by Poisson (Bull. Mus. Hist. Nat. **1**: 278. 1895) and in some species of the nearly related *Cantua*, of the *Polemoniaceae*, there is a woody ridge at the base of each node. The latter, however, is more like the structure which protects the axillary bud in *Syringa* and *Philadelphus* than the spines of the *Fouquieriaceae*.

The majority of the buds in the axils of the primary leaves do not elongate to form branches, but develop small clusters of spatulate leaves which are almost sessile and do not form spines (FIGS. 11 and 12, *c*).

Engelmann (Bot. Gaz. **8**: 338. 1883) was the first to call attention to this peculiar mode of dehiscence of the leaves of *Fou-*

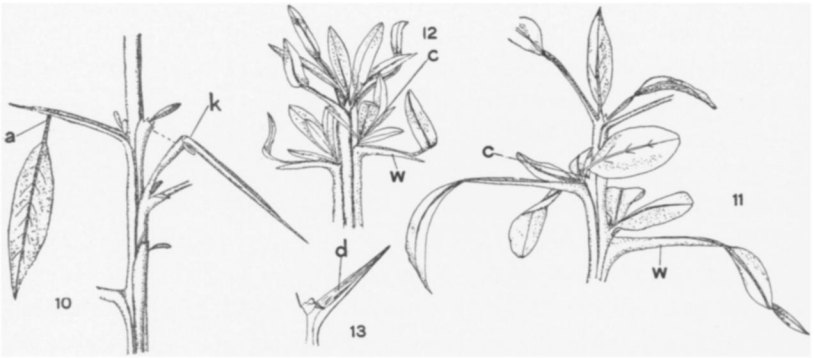

FIG. 10. *Fouquieria Macdougalii*, showing *a*, manner of dehiscence of leaf; *k*, manner in which spine and bark may be peeled from stem.

FIG. 11. Young shoot of *Fouquieria Macdougalii*. *c*, cluster of secondary leaves; *w*, thickening which will form spine.

FIG. 12. Young shoot of *Fouquieria splendens*.

FIG. 13. Spine of *Fouquieria Macdougalii*. *d*, surface from which upper portion of petiole has separated.

quieria. Plank (Garden & Forest, **9**: 73. 1896) says: "The bases of the spines appear to arise in the cellular part, leaving the wood full of holes in their decay," which statement was doubtless made because of the peculiar growth of the cork between the spines and the portions of the outer tissues, which adhere to them, making the spines, with their adhering pieces of bark, dry, papery structures, which still have close enough contact with the adjacent cells to leave a scar when they drop off. Van Tieghem

(Jour. de Bot. **13**: 295. 1899) has described the leaves of the long branches as having sclerenchymatous cells prolonged from the sclerenchymatous layer beneath the epidermis of the stem, on the under side where the epidermis is in contact with the cortex. He considers this subepidermis as the outer part arising from the division of the cortex into two well-differentiated layers, and criticises Baillon (Hist. Pl. **9**: 242. 1888) for referring to the spines as leaves reduced to a midrib. Such a section as that shown in diagram in FIG. 9, where there are several layers of parenchymatous cells between the sclerenchyma (*s*) and the epidermis, shows that the sclerenchymatous cells arise not from a distinct outer layer of the cortex, but within the cortex. Like the prickles of the blackberry and rose, the spines of *Fouquieria* have no vascular tissue, but unlike them, the sclerenchymatous tissue arises from the cortex, not from the cuticle and the abscission layer is nearly at right angles with the axis of the stem instead of being parallel with it and in the surface of the stem.

Various questions naturally arise in the study of such a structure as the spines of the *Fouquieriaceae*. How did these spines originate? Was the stimulus external or internal which caused the original variation? Is *Fouquieria* a genus that was separated from its parent form at a remote period, so that the intermediate forms between it and the other *Polemoniales* have become extinct, or is it a relatively new genus? Is it a stable form, or do the different plants vary in wide range?

Spinose processes are so characteristic of desert flora that the inference was long ago drawn that there is a close association between their structure and environment. The usual corollaries of spine development, reduction in surface and elaborate adaptations for water-holding, as well as the protective character of the spines themselves in warding off the attacks of animals, are such important factors in the maintenance of a genus in arid regions, that it is easy to reason that they are the outcome of influences in those localities external to the plant.

Kerner, Henslow, and others of the older botanists have been inclined to emphasize the principle that "specific forms, on the whole, fit the places they have to live in," rather than their inherent tendency to variation. No experiments have been performed upon

Fouquieria to test the effect of changed climatic conditions upon it, but it has been observed that in greenhouses the leaves remain attached to the plant a number of months, while in nature they are usually cast off at the end of a few weeks ; and in some years, in the wild state, no leaves are produced. Lothelier's experiments upon the barberry (Rev. Gén. Bot. **2**: 276. 1890) showed that when grown in moist air it loses its spines. Henslow (Jour. Linn. Soc. Bot. **30**: 223. 1895) has made a similar observation for *Ononis spinosa*, one variety of which living upon sandy shores is covered with spines, but becomes less and less spinose in favorable conditions or under cultivation, and he cites the cultivated apple and pear as similar examples. Miss Dale (Ann. Bot. **15**: 59, 497. 1901) has noted that when tubers of *Dioscorea* sent out shoots in light and without moisture, the leaves were scarcely developed at all, and the same thing may now be observed in the Museum of the New York Botanical Garden, where tubers of *Dioscorea* in the exhibition cases have sent out branches, the leaves of which are greatly reduced.

There is a wide gap between *Fouquieria* and *Cantua*, its nearest relative among the *Polemoniales*, which fact together with the small number of species in the genus, its confinement to a limited area, and its stability may be taken to indicate that it is an old form, though there is no geological record so far as is known of any similar spine-bearing form.